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CONTRIBUTIONS FROM THE ZOÖLOGICAL LABORATORY OF THE MUSEUM OF COMPARATIVE ZOÖLOGY AT HARVARD COLLEGE. E. L. MARK, DIRECTOR. — No. 108.

THE METAMERISM OF THE HIRUDINEA.

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CONTENTS.

I. Introduction.

As long ago as the year 1862 Gratiolet pointed out that in the medicinal leech, *Hirudo medicinalis* L., the successive rings of the body are not all alike, but that they fall into similar groups of five each, which are repeated in regular succession throughout the greater part of the body. He found in each such group a single nerve ganglion and a single pair of nephropores; in other words, he discovered that there was a segmentation of internal organs (metamerism) which agreed not with single external rings but with the groups of rings.

Gratiolet called the groups of rings “zoonites” (somites). He noticed on the exterior of the body two natural landmarks, which indicated to

him their limits. These were, first, some whitish flecks (sensillæ) found dorsally on the ring which contains the ganglion (sensory ring); secondly, a pair of pores (nephropores) lying in the furrow just posterior to ring 5, counting the sensory ring as ring 1.

Gratiolet seems to have assumed that these convenient landmarks indicated respectively the anterior and posterior limits of the morphological units or somites. In this assumption nearly all subsequent investigators have followed him unquestioningly. Vaillant ('70) alone expressed the view that it would be more logical to look for septa, which should, as in the Chætopoda, mark the limits of the somites. In the case of Pontobdella, Vaillant believed that he had succeeded in finding such septa, but subsequent investigators do not agree with him in this view.

Gratiolet further observed that toward the ends of the body the number of rings in a somite becomes smaller, and the ganglia are crowded closer together. He suggested that the terminal ganglion at either end of the body probably had resulted from a fusion of originally distinct ganglia, as is the case with the ganglia of certain Mollusca (*Helix*, etc.).

Gratiolet thus opened the way for a study of the metamerism of the leech in two directions: first, to determine the number of primitive somites present in the body of the leech; and secondly, to determine the natural limits of these somites. The first problem indicated has received a satisfactory solution through the splendid work of Whitman ('92) on the Rhynchobdellidæ, and of Bristol ('99) on the Gnathobdellidæ.

From studies of my own, the results of which are in process of publication, I can confirm the conclusion of these investigators, that the body of the leech contains thirty-four distinct somites.

The second problem, namely, the determination of the true limits of the somite, has, as already indicated, received practically no attention. To a discussion of this problem and some considerations growing out of it, I now invite attention.

II. Limits of the Somite in the Rhynchobdellidæ.

1. *Neuromeres as a Criterion of Somite Limits.*

In determining the *number* of somites found in the body of the leech, it has been found necessary to rely solely on a study of the nervous system. It would seem natural, therefore, to look in the same direction for a solution of the problem concerning the *limits* of the somite.

Whitman ('92) has shown that in the genus Glossiphonia (Clepsine) each distinct ganglion gives off three pairs of nerves, which are distributed respectively to the ring in which the ganglion typically lies (sensory ring), the ring before it, and the ring behind it (Fig. 1, VIII.).*

If we take neuromeres as criteria of somites, the three rings thus innervated from a common source should be regarded as constituting a somite. According to the commonly accepted view, however, the last two of these rings with the next following ring of the body, *which is innervated from a different ganglion*, represent a somite. See Figure 1, VII′.

The only other view possible would be to regard the somite as composed of a sensory ring and the two rings which *precede* it, but I am not aware that such a view has ever been suggested, and I am unacquainted with any facts which could be presented in its support. Accordingly discussion may be limited to the two views before stated, which are graphically presented at the right and left margins respectively of Figure 1.

a. Somite Reduction in Glossiphonia.

What first suggested to me the possibility that neuromere limits may coincide with somite limits, was a study of the method of somite reduction at the ends of the body of Glossiphonia. See Figure 1, I.–IV.; Figure 2, XXV.–XVII. In the regions indicated the metameric sense organs occur, not as in the middle of the body on every third ring, but on every second ring, or even on successive rings. This fact shows that in those particular regions the somite contains but two rings, or, in extreme cases, only one. If we regard such somites as having had originally each its full quota of three rings, we must suppose that one or two of the three primitive rings have subsequently disappeared. This disappearance might be explained as due either to a complete suppression of a ring or to its fusion with an adjacent ring. A comparative study of the abbreviated somites in different species of Glossiphonia shows that the latter process is invariably the *first step* in the abbreviation of a somite. An examination of Figures 1 and 2 will make this clear. In the case of somite IV. (Fig. 1) a fusion has taken place between the sensory ring and the ring which precedes it. A similar union has occurred in somites III. (Fig. 1) and XXV. (Fig. 2). In the case of

* This leaves out of account a branch (*d*, Fig. 1) which arises from the posterior of the three nerves and is distributed to sense organs on the dorsal surface of all three rings innervated by the ganglion.

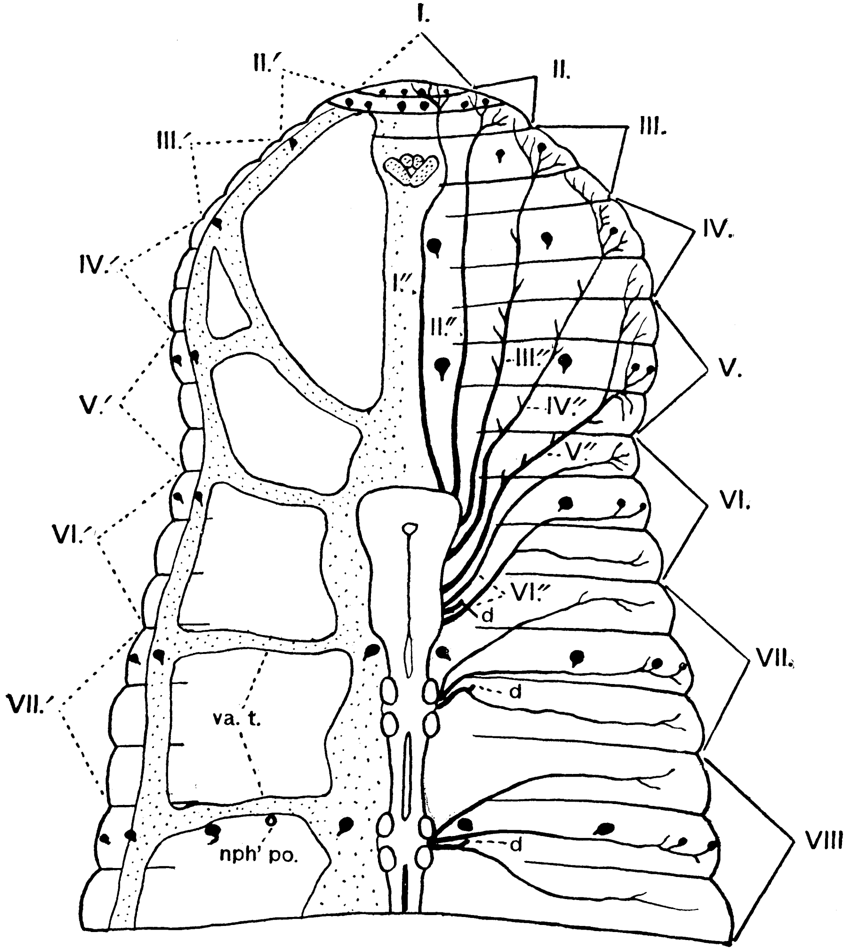

Fig. 1. Dorsal view of the anterior part of the body of *Glossiphonia parasitica* Say (*Clepsine hollensis* Whitman), showing in the right half of the figure the nervous system; in the left half, the lymph system (stippled). The pear-shaped dark bodies shown on certain rings are dorsal sense organs. *d.*, stump of a nerve branch which innervates dorsal sense organs on all three rings of a somite. *nph'po.*, nephropore. *va.t.*, transverse lymph vessel. Somite limits are indicated by roman numerals, at the left of the figure (I.–VII.′), according to Whitman's view; at the right (I.–VIII.), according to the view of the writer. After Whitman ('92), simplified.

somites I. and XXVII. a fusion has taken place between the sensory ring and *both* the adjacent rings, the one which follows as well as the one which precedes it. An intermediate condition is found in somites II., XXV., and XXVI., where the ring following the sensory ring is

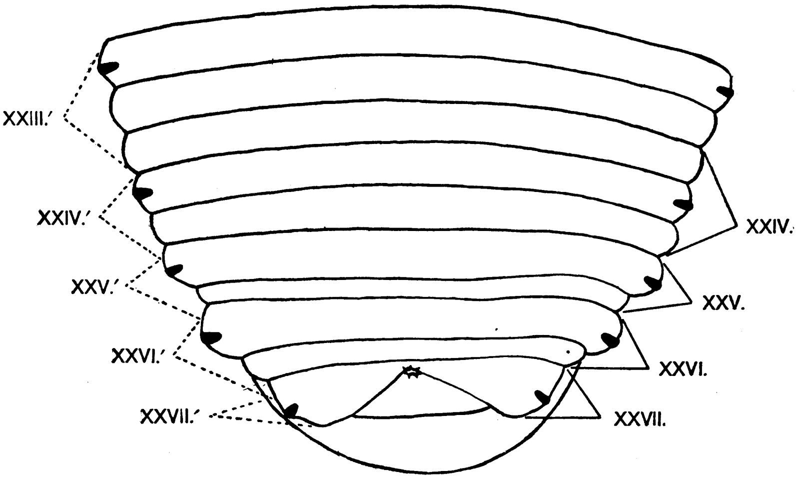

Fig. 2. Posterior end of the body of *Glossiphonia stagnalis* L. (*Clepsine bioculata* Sav.), dorsal view. Somite limits as commonly placed are shown at the left of the figure (XXIII.′–XXVII.′); as the writer would place them, at the right (XXIV.–XXVII.).

considerably reduced in size, but still distinct from the sensory ring anterior to it. The amount of shortening which the somite undergoes is thus seen to be increasingly greater as one progresses from the middle toward either end of the body. The successive steps of abbreviation are: —

1. A fusion takes place between the sensory ring and the ring which precedes it.
2. The ring which follows the sensory ring is reduced in size.
3. It fuses with the sensory ring preceding it.

Accordingly, at the conclusion of this process, we find united in a single ring three primitively distinct rings, — a sensory ring and the two rings adjacent to it. *But these three rings are typically innervated from the same ganglion* (Fig. 1, VII., VIII.). This fact substantiates the view already expressed, that *neuromere limits coincide with somite limits.*

If we do *not* admit that neuromere limits coincide with somite limits,

Whitman's ('92) theory that all the somites of the body are of equal morphological value becomes untenable. For, suppose the body to contain thirty-four distinct ganglia, each innervating three separate rings (the hypothetical primitive condition realized in all unabbreviated somites). Now if the somite limits be marked off so as to include in a somite a sensory ring and the two rings following it, as is the practice of Whitman and others (Fig. 3, left half, compare Fig. 1, left half), we shall have the absurdity of a ring at the anterior end of the body belonging to *none* of the thirty-four somites, and somite XXXIV. at the posterior end of the body will contain *only two rings*. On the other hand, if neuromere limits and somite limits are regarded as coinciding, all somites of the body are of equal morphological value, each somite consisting of three rings innervated from a single ganglion (Fig. 3, right half).

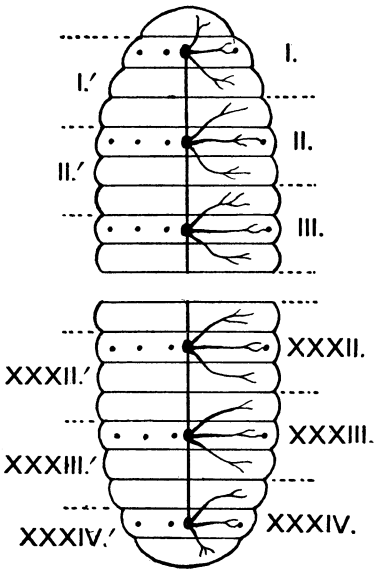

Fig. 3. Diagram showing the relation between neuromeres and somites in the body of a leech with three-ringed somites, — at the left of the diagram (I.′–XXXIV.′), according to the view of Whitman; at the right (I.–XXXIV.), according to the writer's view.

2. *Septa and other Metameric Organs as Criteria of Somite Limits.*

If we are unwilling to be guided solely by the nervous system in determining somite limits, what other criterion can we find? Vaillant ('70) suggested a search for septa. But septa such as are found in Chætopoda are wanting in the leech, unless we so regard the entire blocks of mesodermal tissue which lie between the transverse lymph vessels. The position of the lymph vessels is indicated by stippling in the left half of Figure 1 in the case of *Glossiphonia parasitica* Say (*Clepsine hollensis* Whitman). The transverse lymph vessels are found regularly in the *sensory* ring of each somite (Fig. 1, *va. t.*). It is generally admitted that the lymph vessels represent a greatly reduced cœlom. The blocks of tissue between the transverse vessels are, then, morphologically equivalent to the septa of Chætopoda. But the middle of each such block falls

midway between the sensory rings, exactly the position indicated for the somite limits by the study of the nervous system (Fig. 1, right half).

In his work on "The Embryology of Clepsine," Whitman ('78) states that the testes appear in the septa between the mesodermal somites. Now the position of the testis in the adult is regularly in the two non-sensory rings, that is, exactly midway between successive sensory rings. This is just the position in which the boundary between somites should be on the grounds already examined.

Crop diverticula are repeated at metameric intervals throughout the middle part of the body in most species of Glossiphonia. They invariably arise, so far as my observations go, in the sensory ring of the somite, a fact readily explained by the occurrence in that position of the interseptal portions of the cœlom, represented by the transverse lymph vessels.

There is one other set of organs which is metameric in its arrangement, — the nephridia. A single nephridium, according to the account of Oka ('94), lies principally in the ring which contains the nephropore (sensory ring, Fig. 1, *nph'po.*) and in the two rings which precede it. Accordingly the nephridium is not confined to a single somite, either as somites are commonly limited or as I have suggested placing their limits. This need not surprise us, since in the Chætopoda also the nephridium lies partly in the somite *preceding* that in which the greater part of it is found.

III. Limits of the Somite in the Gnathobdellidæ.

Let us next inquire whether the suggested criteria of somite limits are applicable also in the case of the Gnathobdellidæ.

1. *Relation of Five-ringed to Three-ringed Type of Somite.*

Whitman suggested and Bristol ('99) has demonstrated that the five-ringed type of somite, found in the Gnathobdellidæ, may be derived from the three-ringed type, found in the Rhynchobdellidæ, by supposing that each of the two non-sensory rings of the latter type has divided, while the sensory ring has remained unchanged.

A comparison of the distribution of the nerves arising from a single ganglion in Glossiphonia (Fig. 1) and in Nephelis (Fig. 4) shows the correctness of the homology suggested. The anterior two of the three metameric nerves of Glossiphonia are united in the case of Nephelis (Fig. 4, *a*). They are distributed, as we should expect, to the sensory ring and the two rings which precede it. The posterior nerve of Glossi-

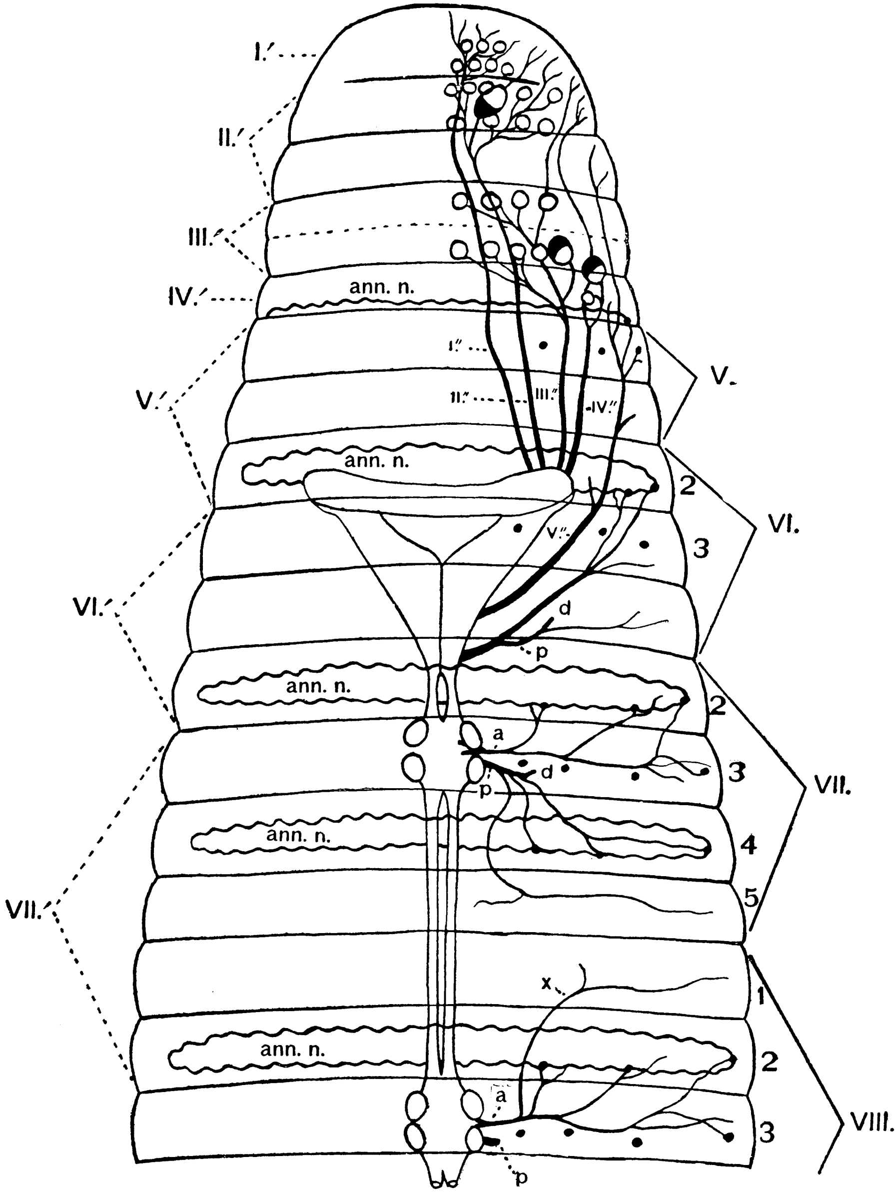
I.′
II.′
III.′
IV.′
V.′
VI.′
VII.′
ann. n.
ann. n.
ann. n.
ann. n.
ann. n.
I.″
II.″
III.″
IV.″
V.″
V.
VI.
VII.
VIII.
d
p
a
d
p
x
a
p
2
3
2
3
4
5
1
2
3

FIGURE 4.

Fig. 4. The first seven somites and part of the eighth somite of *Nephelis lateralis*, dorsal view. *a.*, anterior nerve; *d.*, dorsal branch of posterior nerve, which supplies nervous structures in all five rings of a somite; *ann. n.*, nerve ring found typically in each of the two annuli adjacent to a sensory annulus; *p*, posterior nerve; *x*, a branch of the anterior nerve which ramifies in annulus 1 of its somite.

Roman numerals indicate the somite limits, at the left of the figure (I.′–VII.′), according to the view of Bristol; at the right of the figure (I.–VIII.), according to the writer's view. After Bristol ('99), simplified.

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phonia (Fig. 1) retains its separateness in Nephelis, and is distributed chiefly to the two rings which follow the sensory ring. In Glossiphonia the posterior nerve gives off a branch (*d*, Fig. 1), which is connected with sense organs on the dorsal surface of all three rings. In Nephelis the posterior nerve gives rise to a homologous branch (*d*, Fig. 4), which is distributed to sense organs on the dorsal surface of rings 1, 3, and 5, and is also connected with the nerve rings (*ann. n.*, Fig. 4) discovered by Bristol in rings 2 and 4.

Hence, if neuromere limits coincide with somite limits, the latter must fall, in the case of somites VI.–VIII. of Nephelis, as indicated in the *right* half of Figure 4.* Bristol, working on the basis of Gratiolet's conception, that the sensory ring occurs at the anterior end of the somite, places the somite limits as shown in the *left* half of Figure 4.

2. *Somite Reduction in Nephelis.*

An examination of the abbreviated somites at the ends of the body should, as in the case of Glossiphonia, throw light on the question whether somite limits and neuromere limits are identical.

Giving attention first to the anterior end of the body, somite VIII., as I place the somite limits (Fig. 4, *right* half), is the most anterior unabbreviated somite in the body of Nephelis. In the case of somite VII., ring 1 has disappeared. For, the nerve branch (*x.*, somite VIII.) which typically ramifies in ring 1 is wanting in somite VII. Moreover the most anterior annulus of somite VII. is shown to be homologous with annulus 2 of somite VIII. by the fact that it contains the anterior nerve

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* No entire unabbreviated somite is shown in Figure 4, but the structure of a typical somite may be learned from a study of the last six rings of the figure, which represent unabbreviated the sensory ring and the two following rings of somite VII., and the sensory and two *preceding* rings of somite VIII.

ring of the somite (*ann. n.*), a structure typically found in annulus 2 (see somite VIII., Fig. 4).

Somite VI. clearly consists of three annuli, of which we can identify 3 and 2 by the dorsal sensillæ and the anterior nerve ring respectively. In place of annuli 4 and 5 we have in somite VI. a single annulus, in which, however, Bristol found no nerve ring.

Somite V. consists, apparently, of two annuli. But what the distribution of nerve V.″ shows to be undoubtedly the anterior nerve ring of this somite lies just within the limits of the next anterior annulus (IV.′, left half of Fig. 4). Our first impulse would be to include that annulus in somite V.; but a careful study of the distribution of nerves I.″–IV.″ shows that the annulus in question contains important structures (including the eye and associated sense organs) belonging unquestionably to somite IV. It is possible to suppose that in this case the most anterior part of somite V. has fused with somite IV. It seems to me, however, more reasonable to explain the condition as illustrating a general tendency in the head region for *nerves* to be carried forward of the somites to which typically they would be limited. For example, nerve V.″ (Fig. 4) is carried forward ventrally as far as the last annulus of somite II.; nerve IV.″ runs into the anterior annulus of somite II.; nerves II.″ and III.″ are carried forward into somite I. In Glossiphonia (Fig. 1) also a similar tendency can be recognized in the distribution of nerves III.″–V.″ The nerve ring found in the posterior portion of the annulus assigned by Bristol to somite IV. (Fig. 4, left half) cannot reasonably be considered the posterior nerve ring of somite IV., because it is connected *exclusively* with nerve V.″ (See Bristol's Pl. VII., Fig. 16.) Moreover the posterior nerve ring has disappeared in somites V. and VI., we should therefore expect to find it wanting also in the more abbreviated somite IV. Finally, unless this nerve ring does belong to somite V., that somite contains no nerve ring at all, and somite IV., which is much more extensively abbreviated, still retains a nerve ring. This seems very improbable, for we find that metameric structures omitted from an abbreviated somite, do not appear in other somites still more strongly abbreviated.

In determining the external limits of somites I.–IV., Bristol has been guided by the position of the metameric sense organs and the distribution of the metameric nerves I.″–IV.″, which represent the nerves given off from one side of primitive ganglia I.–IV. respectively, completely fused into single trunks. The somite limits indicated by him in the case of these four metameres are, accordingly, *neuromere* limits, and, so far as I

can judge from second-hand knowledge of the subject, are entirely accurate.

A comparison of Figures 1 and 4 shows that abbreviation has been more extensive in the head end of Nephelis than in that of Glossiphonia. The process also does not progress anteriorly with such even and regular gradations as in the case of Glossiphonia. Nevertheless, abbreviation takes place in both cases by practically the same steps. First the anterior end of the somite is affected, then the posterior end.

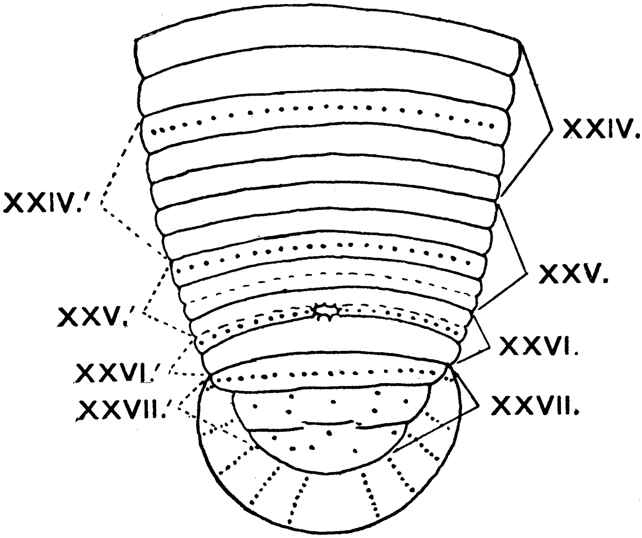

Fig. 5. Posterior end of the body of *Nephelis lateralis,* dorsal view. Somite limits according to the view of Bristol are shown at the left of the figure (XXIV.′–XXVII.′); according to the writer's view, at the right (XXIV.–XXVII.). After Bristol ('99).

Figure 5 gives a dorsal view of the abbreviated somites at the *posterior* end of Nephelis. Somite XXIV. (*right* half of figure) is the last unabbreviated somite and shows the typical condition, — a sensory ring in the middle of the somite preceded as well as followed by two non-sensory rings. In somite XXV. (right side of figure), the sensillæ indicating the fixed third ring from which to reckon, rings 4 and 5 are seen to be partially united. In somite XXVI., rings 1 and 2 are completely fused together and imperfectly united with the sensory ring, 3; rings 4 and 5 are likewise fused together, but retain their distinctness

from the sensory ring, 3. In somite XXVII. a complete union has taken place between rings 1–3; rings 4 and 5 are probably represented in the broad, curved part of the body which bears distally the acetabulum. This part is imperfectly divided by transverse creases (shown too distinctly in the figure), but is sharply marked off from the preceding ring.

To recapitulate: — We find in the case of Nephelis the same rules governing the process of somite reduction as in the case of Glossiphonia.

(1). *Rings fuse into groups innervated typically from a common ganglion.* Examples: Figure 5, right half, somites XXV.–XXVII.; Figure 4, somites III. and IV. The union, at the margins of the body, of somite I. with the anterior ring of somite II. presents an apparent exception, but here we have to do with an extreme case, in which *all* the rings of one somite (I.) have fused with one another, and in addition a fusion between successive somites (I. and II.) is foreshadowed.

(2). *The first rings to disappear are those at the ends of the somite,* the anterior end being usually the one which is first affected. Examples: in Figure 4, somite VII. (only the most anterior ring, 1, wanting); somite VI. (a ring wanting at either end of the somite); somite V. (two rings wanting at the anterior end of the somite, only one wanting at the posterior end); in Figure 5, somite XXVI. (rings 1 and 2 fused together and partially united with ring 3, rings 4 and 5 united); somite XXVII. (rings 1–3 united, rings 4 and 5 united).

In somite XXV. alone we have a case where abbreviation affects the posterior part of the somite sooner than the anterior part. But it will be observed that the middle of somite XXV. marks the boundary between the abbreviated and unabbreviated portions of the posterior half of the body. This may explain why in this single instance rings 4 and 5 are reduced, while rings 1 and 2 are unaffected.

From the foregoing facts it appears that in the case of Nephelis as well as of Glossiphonia there are NATURAL *somite limits, which coincide with the limits of the neuromeres.*

IV. Somite Growth.

Having now examined with some care the process of somite reduction in the leech, it may be instructive to study also the reverse process, namely that of increase in the number of rings in a somite. This can best be done by an examination of typical somites from various genera of the two commonly recognized families of leeches.

1. *Rhynchobdellidæ.*

We are already sufficiently familiar with the typical three-ringed somite of Glossiphonia (Fig. 6, *C*). In Hæmenteria, a closely related genus (Fig. 6, *D*), each of the non-sensory rings (1 and 3) is divided ventrally but not dorsally.

Branchellion has a three-ringed somite like that of Glossiphonia, except that the middle (sensory) ring bears a pulsating respiratory vesicle

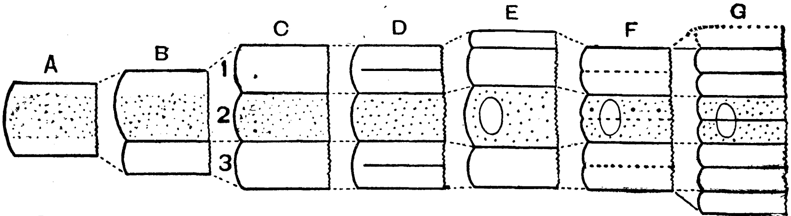

Fig. 6. Somites of Rhynchobdellidæ.
A, a much abbreviated somite of Glossiphonia;
B, a less abbreviated somite of Glossiphonia;
C, a typical somite of Glossiphonia;
D, " " Hæmenteria;
E, " " Pontobdella;
F, " " Trachelobdella;
G, " " Cystobranchus;
The sensory ring and its derivatives are stippled.

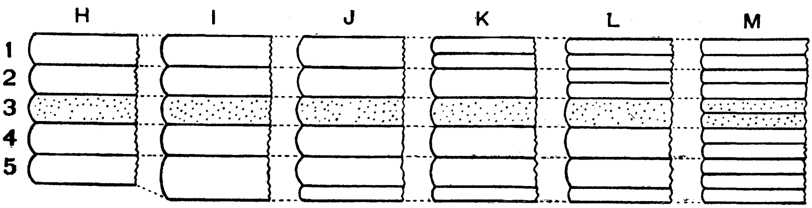

Fig. 7. Typical somites of Gnathobdellidæ. *H*, Nephelis; *I*, Dina; *J–M*, Trocheta. The sensory ring and its derivatives are stippled.

connected with the lymph system. In Ozobranchus, a related genus, one of the non-sensory rings is divided in large individuals. Blanchard ('94), who has described this genus, states that the ring which divides is the *third* ring of the somite, by which I understand him to mean the ring which *precedes* the sensory ring, — ring 1 of my enumeration.

In Pontobdella (Fig. 6, *E*), a typical somite consists sometimes of

three rings, but oftener of four. The sensory ring, which contains a respiratory vesicle, is always the broadest ring of the somite. The ring which is usually present, but sometimes wanting, is a narrow one, which has been added at one end of the somite. It is impossible to say, without studying the nerve distribution, at *which* end it has been added. Apparently, however, it is at the anterior end, for in those animals which I have had an opportunity to examine, the new ring appears to be united more closely with the ring which precedes than with that which follows a sensory ring. Moreover, the ring which precedes the sensory ring is usually not so broad as the one which follows it. This is an indication that it is the former rather than the latter which has undergone division.*

In Trachelobdella (Fig. 6, *F*), according to Blanchard, the somite consists sometimes of three, sometimes of six rings, *each* of the three primitive rings having, in the latter case, divided. The sensillæ remain on the anterior derivative of the original sensory ring.

In Cystobranchus (Fig. 6, *G*) the somite consists of seven rings, two of which bear the respiratory vesicles and doubtless have arisen, as in Trachelobdella, from the division of the original sensory ring. The remaining five rings have probably been derived from the two primitive non-sensory rings, — three from one non-sensory ring, two from the other. One of the non-sensory rings must, accordingly, have divided only once, as in Trachelobdella; the other, twice. The position of the genital pores would seem to indicate that the *posterior* non-sensory ring is the one which has divided a second time; but it is impossible to say without study of internal structures whether this is really the case or not.

A typical somite of Piscicola contains, according to Apáthy ('88), twelve annuli; according to Blanchard ('94), fourteen. Not having had an opportunity to examine this genus myself, I do not venture to express an opinion as to the number or morphological value of the rings. Blanchard, however, states that the respiratory vesicle is borne on *two rings* of the somite, the anterior of which contains the nephropore. This would seem to indicate that the sensory ring had divided only once, and that the remaining twelve rings (or ten, Apáthy) had arisen by repeated division of the two primary non-sensory rings.

To recapitulate: — We find in the Rhynchobdellidæ that, starting with a somite of three rings of equal width, increase in the number of annuli

* Vaillant ('70), who was guided by the position of the "septa," also placed the somite limits so as to make two rings precede the sensory ring and one follow it.

takes place (1) most often by division of one or both of the non-sensory rings; (2) occasionally by division of the sensory ring also. In other words, ring multiplication is most active at the ends of the somite.

2. *Gnathobdellidæ.*

The typical five-ringed somite of Nephelis, Hirudo, and other genera of Gnathobdellidæ (Fig. 7, *H*) has undoubtedly been derived from a three-ringed somite through division of each of its non-sensory rings. This idea, suggested by Whitman ('92), has been abundantly confirmed by the careful work of Bristol ('99).

In the two genera Dina and Trocheta, as described by Blanchard ('94), we find a further multiplication of annuli taking place. In the former genus (Fig. 7, *I*), the last of the five rings which, according to my view, constitute a somite (ring 5, Fig. 7, *I*) is broader than any of the others and is partially divided by a transverse furrow (not shown in the figure). In Trocheta (Fig. 7, *J*) the fifth ring is completely but unequally divided, the posterior of the two rings thus formed being narrower than its mate. Sometimes no further evidences of ring multiplication are found in the somite of Trocheta, but usually other divisions occur forming a somite of seven (Fig. 7, *K*) or more frequently of eight rings (Fig. 7, *L*). Next in order after the division of ring 5 comes that of ring 1 (Fig. 7, *K*), then that of ring 2 (Fig. 7, *L*). Blanchard finds that individuals obtained from the Crimea often show evidence in certain somites of still further divisions affecting the sensory ring and the two broad rings which follow it. This brings the number of rings in the somite up to eleven (Fig. 7, *H*).

It is interesting to note how these eleven rings are related to the three primary rings of a typical somite of Glossiphonia. The primitive sensory ring of Glossiphonia (2, Fig. 6, *C*) is represented in Trocheta by two narrow rings (stippled in Fig. 7, *M*). It may, therefore, be regarded as having divided *once*, the division being among the latest to occur in any of the rings. In place of ring 1 of Glossiphonia (Fig. 6, *C*), there are four rings in Trocheta (Fig. 7, *M*). Primitive ring 1 may accordingly be said to have divided *twice* (compare Figs. 6, *C*; 7, *H*; and 7, *M*). In place of ring 3 of Glossiphonia (Fig. 6, *C*), we find in Trocheta (Fig. 7, *M*) five rings; in other words, the primitive posterior ring of the somite has divided *twice*, and the most posterior of the four rings thus formed has divided a *third time* (compare Figs. 6, *C*; 7, *H*; 7, *J*; and 7, *M*).

To recapitulate: — In ring multiplication among the Gnathobdellidæ (1) all five rings occasionally divide; (2) more often only the non-sensory rings divide, the sensory ring remaining unaffected; (3) division takes

place *first* and most often in those rings which stand at the limits of the somite (rings 1 and 5, Fig. 7).

If one marks off the somite limits in any other way than that which I have followed, regarding the sensory ring either as the first or as the last ring of the somite, the process of ring multiplication becomes unintelligible, taking place now in the middle, now at one end of a somite. The reader can test this for himself by reconstructing the diagrams given in Figures 6 and 7 so as to make the stippled ring come at one end or the other of the somite.

From the foregoing discussion the conclusion seems warranted that *neuromeric groups of rings,* that is, rings innervated typically from the same ganglion, *are natural groups behaving as units both in the process of abbreviation and in that of elongation* of particular body regions; in other words, that *they are the true morphological units or somites.*

V. Primitive Condition of the Leech Somite.

We have seen that the process of ring multiplication is very general among the leeches, and that it takes place in quite an orderly manner, new annuli being formed, in the great majority of cases, at the ends of the somite. We have seen, further, that the complicated forms of somite found in the Gnathobdellidæ and some of the Rhynchobdellidæ are all derivable from a primitive three-ringed type of somite, like that of Glossiphonia. In view of these facts, does it not appear probable that the three-ringed type of somite itself has been derived from a simpler primitive condition? I am strongly inclined to think so.

As to what this simpler condition was, we perhaps may get an idea from an examination of the abbreviated somites of Glossiphonia (Fig. 6, *B*, *A*). For we have found that multiplication of annuli is the reverse process of somite reduction, both alike affecting the *ends* of the somite, the sensory (middle) ring being the stable component of the somite in changes of either sort.

The final result of somite reduction in Glossiphonia (Fig. 6, *A*) points to a primitive condition of the leech somite, in which it consisted, like the somite of a chætopod, of a single ring. A tendency to increase the number of annuli in the somite would, in harmony with what we know of the process of ring multiplication in the leeches, have called for the formation of a new and narrower ring at one end or the other of the somite, or at both. If new rings were formed simultaneously at both ends of the primitive one-ringed somite, we should arrive, by a single step, at substantially the condition of somite found in Glossiphonia (Fig. 6, *C*).

If, however, a new ring were formed first at only one end of the somite, the probabilities are that it would be at the posterior end. For we have found that ring multiplication occurs rather oftener there than at the anterior end of the somite. Moreover, in somite reduction in Glossiphonia, we get a stage (Fig. 6, *B*) intermediate between the one-ringed (Fig. 6, *A*) and three-ringed (Fig. 6, *C*) condition of the somite, in which rings 1 and 2 are united into a single broad anterior ring, while ring three is entirely distinct.

The intermediate condition just described not improbably represents a true phylogenetic stage in the formation of the three-ringed type of somite, for it corresponds exactly with the condition found in a typical body somite of Branchiobdella or of Bdellodrilus (Fig. 8), those curious leech-like annelids, which nevertheless possess certain chætopod characters. The ganglion (*g.*, Fig. 8) of a somite of Bdellodrilus or Branchiobdella is situated, as we should expect if the views just expressed are correct, in the broader anterior ring of the somite. This ring, according to the homology suggested, corresponds with rings 1 and 2 of Glossiphonia (Fig. 6, *B* and *C*).

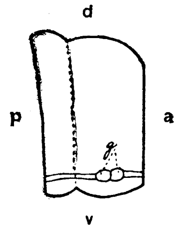

Fig. 8. A single body somite of *Bdellodrilus illuminatus*, lateral view. *a.*, anterior; *d.*, dorsal; *g.*, ganglion; *p.*, posterior; *v.*, ventral. After Moore ('95).

If, as I believe, the common assumption is well grounded, that leeches and chaetopods have been derived from a common stock, can we discover any reason why ring multiplication should take place in one group and not in the other? I think we have a sufficient explanation in the fact that the leech body contains always the same definite number of somites, no matter how large or how small the animal may be. This number is thirty-four, both in the Rhynchobdellidæ and in the Gnathobdellidæ.

In the chaetopod, on the other hand, the body contains at first a relatively small number of somites, which is increased, as the animal grows in size, through the formation of new somites in some limited region of the body, usually at its posterior end. In some cases the newly formed somites may separate themselves off as a distinct individual, in other cases they serve merely for the elongation of the original individual to an indefinite extent.

In the leech, however, there is no provision for increase in the number of somites. A definite number of somites, thirty-four, is laid down early in ontogeny, and never increased. Elongation of the body

takes place, therefore, only by elongation of the individual somites which compose it. This method of growth is probably what has called forth the phenomenon of ring multiplication. In support of this view may be cited facts such as that stated by Blanchard ('94) in regard to Ozobranchus, that one of the three rings of a typical somite is *doubled in the case of large individuals.*

SUMMARY.

1. The *number* of somites in the body of the leech has been determined correctly by Whitman ('92) for the Rhynchobdellidæ, by Bristol ('99) for the Gnathobdellidæ. In both cases the number is thirty-four.

2. The *limits* of the leech somite have been placed incorrectly by all students of leech metamerism, with the possible exception of Vaillant ('70) in the case of a single genus, Pontobdella, from the time of Gratiolet ('62) to the present.

3. The natural and true limits of the somite coincide with the limits of the neuromere; that is, a somite includes those annuli which typically are innervated from the same nerve ganglion.

4. The foregoing statement is confirmed by an examination of metamerically repeated structures other than ganglia; namely, septa, testes, and crop diverticula.

5. Neuromeric groups of rings, that is, somites as defined under 3, behave as structural units (*a*) in somite abbreviation (reduction in the number of rings in a somite), (*b*) in somite elongation (increase in the number of rings in a somite).

6. Both reduction and increase in the number of rings take place chiefly at the ends of the somite. The sensory ring occupies the middle of the somite and is least often and least extensively affected in the two processes just named. It represents the *stable* component of the somite.

7. The five-ringed type of somite found in the Gnathobdellidæ has been derived from the three-ringed type found in the Rhynchobdellidæ, as suggested by Whitman and demonstrated by Bristol. This has been brought about by division of the non-sensory ring at either end of the somite.

8. The wide prevalence of ring multiplication among the Hirudinea suggests the derivation of the three-ringed type of somite from a still simpler type consisting, as in Chætopoda, of a single ring.

9. A phylogenetically intermediate stage between the one-ringed and three-ringed types of somite is probably represented in a typical body somite of Branchiobdella. The same type of somite structure appears

also in the abbreviated somites of Glossiphonia, as a stage intermediate between the three-ringed and one-ringed conditions of the somite.

10. The phenomenon of ring multiplication in the Hirudinea is correlated with the restricted number of somites found in the body. Increase in the number of somites does not take place in the body of the adult leech. Without this, elongation of the body is possible only through lengthening of individual somites. Lengthening of the individual somite has probably been the cause, phylogenetically, of increase in the number of rings in a somite.

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